PROC. ENTOMOL. SOC. WASH.
98(4), 1996, pp. 667–676

LARVAL FEEDING AND DEVELOPMENT OF *LEUCOPIS NINAE* TANASIJTSHUK AND TWO POPULATIONS OF *LEUCOPIS GAIMARII* TANASIJTSHUK (DIPTERA: CHAMAEMYIIDAE) ON RUSSIAN WHEAT APHID, *DIURAPHIS NOXIA* (MORDVILKO) (HOMOPTERA: APHIDIDAE), IN WASHINGTON

STEPHEN D. GAIMARI AND WILLIAM J. TURNER

Department of Entomology, Washington State University, Pullman, WA 99164-6382, U.S.A.; SDG, current address: Department of Entomology, 320 Morrill Hall, 505 South Goodwin Avenue, University of Illinois, Urbana, IL 61801, U.S.A.

Abstract.—Three populations of *Leucopis* (Diptera: Chamaemyiidae), including *L. ninae* Tanasijtshuk and two populations of *L. gaimarii* Tanasijtshuk, were studied to determine their relative larval development times and feeding rates at different temperatures. Using three experimental temperatures (20.0°, 23.3°, 26.6°C), we determined that the developmental times of all three populations significantly decreased with increasing temperature. Additionally, the number of aphids consumed per day significantly increased from the lowest to the highest experimental temperatures for each population. There were few differences among the three populations for the aspects studied, although one population of *L. gaimarii* had a significantly ($P > 0.005$) longer third stadium (and total larval duration) at the lowest experimental temperature than either *L. ninae* or the other population of *L. gaimarii.* This coincided with a higher mean number of aphids consumed for this population at this temperature. Most importantly, we found that these *Leucopis* species are voracious predators on aphids, with each individual killing approximately 100 aphids throughout larval life. Also, our data suggests that the species native to the Pacific Northwest, *L. gaimarii,* is as effective a predator on the Russian wheat aphid as the introduced species, *L. ninae.*

Key Words: Chamaemyiidae, *Leucopis,* larval feeding, larval development, Aphididae, *Diuraphis noxia,* Russian wheat aphid, biocontrol

All larval Chamaemyiidae that have been studied are predators on soft-bodied homopterans, particularly those in the superfamilies Aphidoidea and Coccoidea. Because this group of flies is potentially useful in biological control programs targeting aphids, adelgids, scales, and mealybugs (Balch 1952, Balch et al. 1956, Brown and Clark 1957, Clark and Brown 1962, Culliney et al. 1988, Delucchi and Pschorn-Walcher 1954, Eichhorn 1968, Gaimari 1991, Greathead 1995, Mills 1990, Nakao et al. 1981, Stevenson 1967, Tanasijtshuk 1986, Tiensuu 1951, Tracewski 1983, Wilson 1938), there is a need for more information on larval feeding and development.

Besides a general understanding of the Chamaemyiidae as predators of soft-bodied homopterans, the feeding habits are poorly understood. Some, but not all, genera have been associated with particular groups of homopterans, e.g. *Chamaemyia* Meigen and *Parochthiphila* Czerny on mealybugs of grasses and *Neoleucopis* Malloch on Adel-

gidae. However, most species within the family have never actually been associated with particular hosts, and very few biological observations have been recorded. Specific larval feeding habits have been recorded for very few of the known Nearctic species of the genus *Leucopis* Meigen (Bennett 1961, Gaimari 1993, Maple 1934, McAlpine and Tanasijtshuk 1972, Sluss and Foote 1971, 1973, Tracewski 1983). Tanasijtshuk (1986) summarizes much of the known information for Palearctic species of this and other genera, including host ranges. Additional biological information is available for certain species of *Chamaemyia* (Raspi 1983, Tanasijtshuk 1970b), *Leucopis* (including all the subgenera) (Cherian 1933, Cottam 1922, McAlpine 1977, 1978, Raspi 1983, Sandhu and Kaushal 1975, Tanasijtshuk 1959, 1961, 1962, 1970a, 1972, Tawfik 1965, Valenti and Gaimari 1992), *Leucopomyia* Malloch (Babaev and Tanasijtshuk 1971, Tanasijtshuk 1965), *Lipoleucopis* de Meijere (Wilson 1938), *Melaleucopis* Sabrosky (Beingolea 1957), *Neoleucopis* (Brown and Clark 1957, Clark and Brown 1957, McAlpine 1971), *Parochthiphila* (Raspi 1983, Tanasijtshuk 1963, 1968), and *Pseudodinia* Coquillett (Barber 1984, 1985).

This paper provides information on two species of *Leucopis* (*s. str.*), namely *L. ninae* Tanasijtshuk from Skopje, Macedonia (approximately 42°N 21°E) and two populations of *L. gaimarii* Tanasijtshuk from eastern Washington (Gaimari 1993, Gaimari and Turner 1996, Tanasijtshuk 1996). We compared their developmental times at three temperatures for all larval instars and the puparial stage. We also compared their larval feeding rates on *D. noxia,* and their total aphid consumption in controlled conditions. At the time of this study, *L. ninae* was first being released against *D. noxia* in the Pacific Northwest by USDA-APHIS-PPQ (Prokrym et al., in press). The life history information and observations presented herein points to the usefulness of pre-release comparisons of the biology of exotic predators slated for release with their native congeners.

Materials and Methods

The *Leucopis* species were maintained in the Northwest Biological Control Insectary and Quarantine at Washington State University, and *D. noxia* were from a USDA-ARS colony. The 'Central Ferry' population of *L. gaimarii* (*L.* sp. #1 of Gaimari [1993]) originated in Washington, Garfield County, Central Ferry, USDA-ARS Research Farm (46°37′N 117°49′W; elevation 195 m), swept from cereal ryegrass, *Secale cereale* Linnaeus (Poaceae), infested with the Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Homoptera: Aphididae), in July 1991. The 'Anatone' population of *L. gaimarii* (*L.* sp. #2 of Gaimari [1993]) originated in Washington, Asotin County, 0.6 km west Anatone (46°08′N 117°08′W; elevation 1160 m), swept from *D. noxia*-infested wheat, *Triticum aestivum* Linnaeus (Poaceae), in August 1991. Additional information on the origins and maintenance of the fly and aphid colonies can be found in Gaimari (1993), but note that all three populations were originally collected in the field from *D. noxia*-infested cereal grasses.

The experimental aphid host-plant was 'Steptoe' barley, *Hordeum vulgare* Linnaeus (Poaceae), chosen for its broader leaf compared with wheat. For a continual supply of plants, we sowed 30 seeds into each of two 13 cm pots every five days, and grew them at 25 ± 5°C under constant light to a height of 15 cm, with the first leaf unfolded (Stage 1 of Feekes Scale [Large 1954]). Plants were then maintained in an experimental growth chamber (23.3 ± 3.4°C; photoperiod of 16:8 h).

We performed experiments at three temperatures (20.0 ± 0.1°, 23.3 ± 0.1°, and 26.6 ± 0.1°C) using illuminated incubators with the same photoperiod as above. At each temperature, there were 15 replicates for *L. ninae* and for each population of *L. gaimarii.* Each replicate required a study apparatus (modified from Barber 1984)

consisting of clear, glass tubing, 15–16 cm in length, with an inner diameter of 0.55 cm and an outer diameter of 0.7 cm. Stiff paper (biological drawing stock) was cut into 13 × 0.65 cm strips, and a single, green, healthy barley leaf was clipped and anchored with nontoxic white glue along its entire length to each paper strip, to prevent aphids from getting under the leaf. The glue was allowed to air dry for 20 minutes, after which the paper strips were curled to permit insertion into the glass tube. Each barley leaf was replaced with a fresh one every two days. Plants of uniform age (10–15 days old) were used throughout the study.

We transferred a single *Leucopis* egg (from a *D. noxia*-reared culture) and 10 *D. noxia* nymphs (third instar or older) to the top surface of each barley leaf, using a 00 camel's-hair brush. Eggs were collected from throughout the rearing cages and from different females. Each leaf was slipped into a glass tube and both ends were plugged with cotton. Each tube was affixed to a number-coded, wooden mount. All apparati were placed on a single shelf in the appropriate incubator.

After egg hatch, we counted and removed all live aphids and carcasses daily to determine the number of aphids killed and consumed by each larva. Shriveled carcasses were considered to have been the result of predation, while the uncommonly encountered entire carcasses were not, as they may have died from other causes. We then added fresh aphid nymphs from the *D. noxia* colony to bring the number in each apparatus to the required quantity as described below.

The number of aphid nymphs provided to the maggots was based on preliminary studies and varied as follows. Throughout the first stadium, 10 aphids were used. The number was increased to 20 for the second stadium (at the highest experimental temperature, the number of aphids supplied here was increased to 30, due to an increased rate of predation). For the third stadium, the number of aphids added each day was increased to 30 (again, at the highest experimental temperature, an additional 10 were provided).

After pupariation, we carefully removed each puparium from the tube by breaking the sticky adhesive that attached them to the substrate (Gaimari 1993). We then moved each into a labeled, plastic, tissue-culture dish and placed them back into the incubator to await adult emergence.

Following adult emergence and tanning, the tissue-culture dishes were dated and stored at −0.5°C. Each adult specimen and its associated puparium was point-mounted on the same insect pin, and placed in the Maurice T. James Entomological Collection at Washington State University.

Statistical analyses were made using a one-factor analysis of variance with repeated measures, comparing: the number of aphid nymphs consumed by each population within a given experimental temperature; the number of aphid nymphs consumed at each temperature within a population; the developmental period between populations within a given experimental temperature; and the developmental period at each temperature within a population. We used Scheffé's F-test to detect differences significant at 95% between populations. For all calculated F-values, df = 2, 28 and, unless stated otherwise, $P < 0.001$.

Results

Developmental time.—Temperature influenced the time spent in each larval instar and puparial stage of the three *Leucopis* populations. In each, the time for completion of each stadium or life stage, in addition to the total time, decreased with increasing temperature (Table 1). This trend is illustrated by the total time required to complete development from egg to adult in each population as temperature increased from 20.0 to 26.6°C (Fig. 1). Within each population, the resulting F-values of the statistical analyses of mean developmental times at the different temperatures are given in Table 2.

Table 1. Mean developmental times ± SE (days) for three *Leucopis* populations. In each row, mean values followed by different lower case letters are different (df = 2, 28; $P < 0.001$; Scheffé's F-test), while in each column (within a stage or instar), mean values followed by different upper case letters are different (see Table 2; Scheffé's F-test). The same letter or absence of lettering denotes no significant difference.

		L. ninae	*L. gaimarii* 'Central Ferry'	*L. gaimarii* 'Anatone'
1st instar:	20.0°C	2.50 ± 0.07 A	2.50 ± 0.07 A	2.57 ± 0.08 A
	23.3°C	2.10 ± 0.10 B	2.07 ± 0.12 B	2.23 ± 0.11 A
	26.6°C	1.70 ± 0.10 C	1.93 ± 0.10 B	1.77 ± 0.10 B
2nd instar:	20.0°C	2.47 ± 0.08 A	2.37 ± 0.08 A	2.37 ± 0.10 A
	23.3°C	2.30 ± 0.14 A	1.97 ± 0.10 B	2.07 ± 0.12 A
	26.6°C	1.20 ± 0.08 B	1.37 ± 0.06 C	1.27 ± 0.10 B
3rd instar:	20.0°C	4.53 ± 0.12 aA	4.60 ± 0.11 aA	5.80 ± 0.18 bA
	23.3°C	3.73 ± 0.19 B	3.87 ± 0.15 B	4.07 ± 0.12 B
	26.6°C	3.20 ± 0.14 B	3.27 ± 0.10 C	3.23 ± 0.14 C
larval total:	20.0°C	9.47 ± 0.19 aA	9.47 ± 0.17 aA	10.73 ± 0.26 b[1]A
	23.3°C	8.10 ± 0.25 B	7.90 ± 0.16 B	8.37 ± 0.23 B
	26.6°C	6.07 ± 0.19 C	6.67 ± 0.16 C	6.27 ± 0.16 C
puparial:	20.0°C	13.20 ± 0.15 A	12.67 ± 0.16 A	12.93 ± 0.21 A
	23.3°	9.93 ± 0.15 B	10.13 ± 0.13 B	10.40 ± 0.13 B
	26.6°C	8.13 ± 0.13 C	7.93 ± 0.15 C	7.93 ± 0.07 C
total:	20.0°C	23.13 ± 0.19 a[2]A	22.40 ± 0.24 aA	24.07 ± 0.28 bA
	23.3°C	18.27 ± 0.27 B	18.20 ± 0.22 B	19.07 ± 0.35 B
	26.6°C	14.27 ± 0.15 C	14.73 ± 0.27 C	14.27 ± 0.12 C

[1] Different at $P < 0.005$; [2] Different at $P < 0.05$.

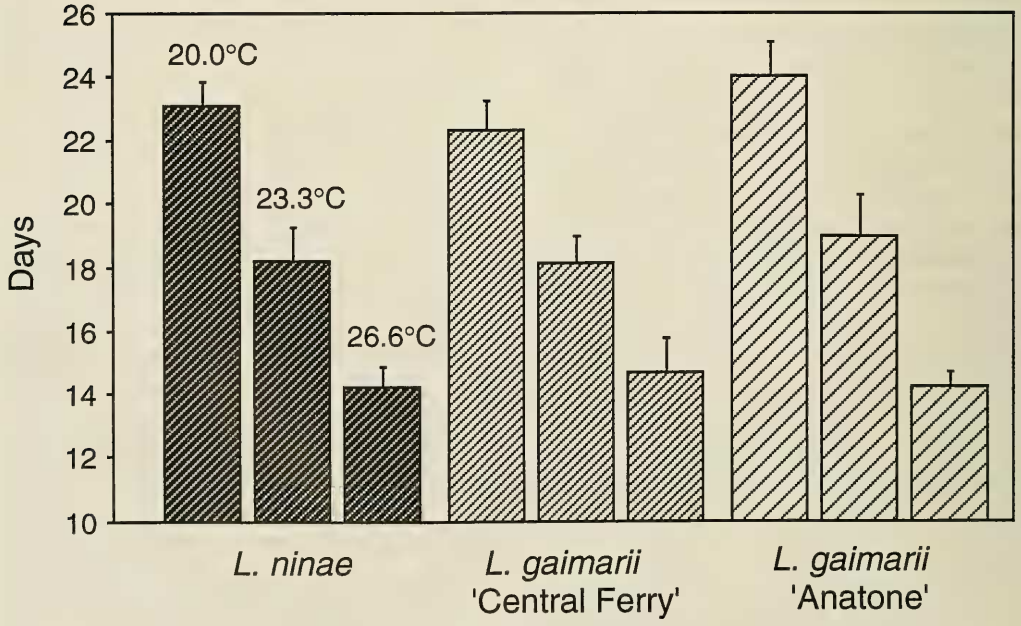

Fig. 1. Total developmental times from egg to adult for *Leucopis ninae* and two populations of *L. gaimarii* at three experimental temperatures. Error bars = SE.

Table 2. *F*-values for the differences in number of *D. noxia* nymphs consumed by each larval instar of three *Leucopis* populations at the three experimental temperatures (df = 2, 28; $P < 0.001$; Scheffé's *F*-test).

		L. ninae	*L. gaimarii* 'Central Ferry'	*L. gaimarii* 'Anatone'
1st instar:	20.0 vs. 23.3°C	4.54[2]	4.05[2]	—
	23.3 vs. 26.6°C	4.54[2]	—	5.50[3]
	20.0 vs. 26.6°C	18.16	6.93[1]	16.17
2nd instar:	20.0 vs. 23.3°C	—	5.48[3]	—
	23.3 vs. 26.6°C	48.45	12.33	14.50
	20.0 vs. 26.6°C	64.25	34.24	27.42
3rd instar:	20.0 vs. 23.3°C	7.21[1]	9.75	29.86
	23.3 vs. 26.6°C	—	6.53[1]	6.90[1]
	20.0 vs. 26.6°C	20.02	32.25	65.46
larval total:	20.0 vs. 23.3°C	14.68	23.60	27.54
	23.3 vs. 26.6°C	32.51	14.62	21.68
	20.0 vs. 26.6°C	90.88	75.37	98.10
puparia:	20.0 vs. 23;3°C	127.97	80.65	64.25
	23.3 vs. 26.6°C	38.86	60.82	60.91
	20.0 vs. 26.6°C	307.86	281.55	250.27
total:	20.0 vs. 23.3°C	189.04	84.88	75.14
	23.3 vs. 26.6°C	127.70	57.83	69.25
	20.0 vs. 26.6°C	627.48	282.82	288.67

[1] Different at $P < 0.005$; [2] Different at $P < 0.05$; [3] Different at $P < 0.01$.

There were no differences in developmental times among the three species at the highest two temperatures, 23.3°C and 26.6°C (see Table 1). At 20.0°C, however, the duration of the third stadium of *L. gaimarii* 'Anatone' was longer than that for either *L. ninae* ($F = 20.83$) or *L. gaimarii* 'Central Ferry' ($F = 18.69$). Subsequently, the entire larval stage of *L. gaimarii* 'Anatone' was longer than that for either of the other two ($F = 8.51$; $P < 0.005$), and the total time from egg to adult was longer for *L. gaimarii* 'Anatone' than for either *L. ninae* ($F = 3.75$; $P < 0.05$) or *L. gaimarii* 'Central Ferry' ($F = 11.95$).

Feeding.—The larval feeding rates (aphids consumed per day) increased as temperature increased from 20.0° to 26.6°C for each species (Fig. 2): *L. ninae* ($F = 60.52$), *L. gaimarii* 'Central Ferry' ($F = 29.03$), and *L. gaimarii* 'Anatone' ($F = 79.33$). However, for each species, the mean number of aphid nymphs consumed (Table 3) by first and second instars and overall did not change with increasing temperature. In the third stadium, by contrast, there was

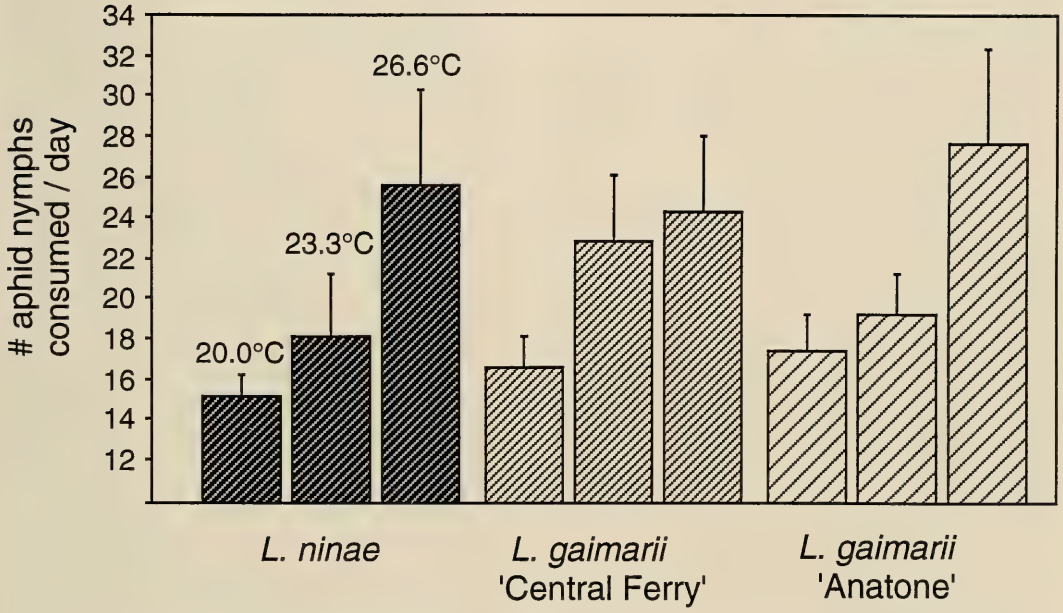

Fig. 2. Mean consumption rates of *Diuraphis noxia* for larval *Leucopis ninae* and two populations of *L. gaimarii* at three experimental temperatures. Error bars = SE.

Table 3. Mean number of *D. noxia* nymphs consumed ± SE, by each larval instar of three *Leucopis* populations. In each row, mean values followed by different lower case letters are different (df = 2, 28; $P < 0.001$; Scheffé's *F*-test), while in each column (within a stage or instar), mean values followed by different upper case letters are different (df = 2, 28; $P < 0.05$; Scheffé's *F*-test). The same letter or absence of lettering denotes no significant difference.

		L. ninae	*L. gaimarii* 'Central Ferry'	*L. gaimarii* 'Anatone'
1st instar:	20.0°C	5.13 ± 0.19	4.93 ± 0.23	5.00 ± 0.20
	23.3°C	4.60 ± 0.27	4.93 ± 0.21	4.73 ± 0.28
	26.6°C	5.20 ± 0.26	5.20 ± 0.24	5.07 ± 0.27
2nd instar:	20.0°C	13.60 ± 0.61	12.53 ± 0.51	12.40 ± 0.59
	23.3°C	13.00 ± 0.79	12.40 ± 0.45	11.13 ± 0.94
	26.6°C	11.60 ± 0.57	11.87 ± 0.39	12.40 ± 0.58
3rd instar:	20.0°C	68.40 ± 1.76 aA	76.20 ± 1.94 aA	100.87 ± 4.52 bA
	23.3°C	67.73 ± 4.60 aA	87.73 ± 4.12 b[1]B	77.60 ± 2.52 abB[2]
	26.6°C	79.67 ± 1.53 B	79.20 ± 3.59 AB	89.07 ± 2.50 B
total:	20.0°C	87.13 ± 1.86 a	93.60 ± 1.84 a	118.27 ± 4.67 b
	23.3°C	85.33 ± 4.46 a	105.07 ± 3.96 b[1]	93.47 ± 2.70 ab
	26.6°C	96.47 ± 1.85	96.27 ± 3.53	106.53 ± 2.69

[1] Different at $P < 0.005$; [2] Different at $P < 0.001$.

some variation with temperature. The number of nymphs consumed by *L. ninae* was higher at 26.6°C than at either 20.0°C ($F = 3.426$; $P < 0.05$) or 23.3°C ($F = 3.843$; $P < 0.05$). For *L. gaimarii* 'Central Ferry', the third instars consumed more aphid nymphs at 20.0°C than at 23.3°C ($F = 3.463$; $P < 0.05$). The highest number of aphid nymphs consumed was by third instars of *L. gaimarii* 'Anatone' at 20.0°C. They consumed more than those at either 23.3°C ($F = 13.354$) or 26.6°C ($F = 3.435$; $P < 0.05$).

At the three temperatures, the mean numbers of aphid nymphs consumed by various instars of the three species (Table 3) did not display a noticeable pattern. At the highest temperature (26.6°C), there were no statistical differences among the three species in the number of nymphs consumed during the larval stages. However, there were differences at the lower temperatures. For example, at 20.0°C, *L. gaimarii* 'Anatone' consumed more aphid nymphs during the third stadium than did either *L. ninae* ($F = 27.80$) or *L. gaimarii* 'Central Ferry' ($F = 16.05$), and larvae of *L. gaimarii* 'Anatone' consumed more total nymphs than did *L. ninae* ($F = 25.22$) or *L. gaimarii* 'Central Ferry' ($F = 15.83$). At 23.3°C, *L. gaimarii* 'Central Ferry' consumed more aphid nymphs than did *L. ninae* in the third stadium ($F = 7.31$; $P < 0.005$) and in the larval stage overall ($F = 7.66$; $P < 0.005$).

Discussion

Developmental times among the three populations did not differ at the two highest temperatures (23.3°C and 26.6°C). At the lowest temperature (20.0°C), however, *L. gaimarii* 'Anatone' required more time to complete the third stadium, coupled with consumption of many more aphid nymphs than either *L. ninae* or *L. gaimarii* 'Central Ferry'. In fact, *L. gaimarii* 'Anatone' consumed more aphid nymphs at 20.0°C than at 23.3°C or 26.6°C, and more than either of the other two at any temperature. This indicates that *L. gaimarii* 'Anatone' may be an effective predator at lower temperatures, with a lower feeding rate but higher total consumption.

Developmental times showed a consistent relationship with the rearing temperatures overall. For each of the three populations, the lowest number of days required to complete development was at the highest temperature (26.6°C). Each stadium was

shortened as the temperatures increased. From these results, one might infer that rearing *Leucopis* can be most quickly achieved at 26.6°C. However, at this high temperature, about half of the trials had to be restarted due to larval death during the first and second stadia. Larval death was less frequent (≈10–20%) at the two lower temperatures. Although not precisely quantified, these data suggest that larvae are less likely to survive at high temperatures (i.e. 26.6°C), but surviving larvae develop faster than conspecifics at lower temperatures. However, our study did not consider the microhabitat conditions in the field. Nor did we attempt to determine oviposition or other rearing factors at different temperatures.

An important finding from this study is that larvae of these *Leucopis* species are voracious predators on *D. noxia.* Larvae of the three populations developed rapidly in an artificial environment and may develop as quickly in the field, if a steady supply of aphids is available. For the three temperatures examined, aphid nymph consumption rates were affected by temperature. As temperature increased, feeding rates similarly increased for all three species, which was coupled with a decrease in the duration of the larval stage.

The information gained in this study is not intended to reflect the true conditions in the larval microhabitat, which are likely much different. Rather, the data serve as a general guideline for comparisons among the populations studied. These comparisons reflect the general feeding trends observed for two native populations of *L. gaimarii* and an exotic species, *L. ninae,* which has been introduced against *D. noxia* since 1991 in Arizona, California, Colorado, Idaho, Indiana, Kansas, Montana, Nebraska, New Mexico, Nevada, Oklahoma, Oregon, South Dakota, Texas, Utah, Washington, and Wyoming (Prokrym et al., in press). The results indicate that under these laboratory conditions the introduced exotic species and its native congener are at least equally effective in terms of larval feeding and development. Because the native species was found to be exploiting the pest resource in the field, i.e. the predator niche was already filled by a native, it seems more important to perform pre-release biological studies comparing its biology with the exotic. These studies should focus on potential advantages that the exotic species may have over its native congener against a particular pest. In this case, the exotic should be able to outperform the native in some aspects of their biology, for example, it should have more efficient feeding, faster development, higher fecundity, or be able to exploit the resource in some way that the native cannot.

This study also serves to further illustrate an idea considered by Gaimari and Turner (1996) based on immature morphology. The two populations of *L. gaimarii* can be distinguished in the immature stages (Gaimari and Turner 1996), while the adults are apparently indistinguishable morphologically (Tanasijtshuk 1996). The current study provides further evidence that the two populations of *L. gaimarii* are distinct, because the 'Anatone' population had a significantly longer developmental period and consumed more total prey at the lowest experimental temperature than did the 'Central Ferry' population. Although we are not suggesting that these populations should be accorded species rank, these biological differences can be considered in an evolutionary context. As was suggested by Gaimari and Turner (1996), the two populations could have recently become separated, perhaps due to host or elevational preferences, and had begun to diverge when *D. noxia* entered the region and provided a suitable, unexploited resource for both of them. Certain developmental differences could have already become established and were partly reflected in this study.

Acknowledgments

This work was part of the Masters degree requirements of S. D. Gaimari. The authors thank the following people from Washing-

ton State University: S. L. Clement, USDA-ARS, for unlimited access to aphids and growth chamber space; T. D. Miller, Northwest Biological Control Insectary, for ideas and help in rearing the flies; D. G. Lester, for making room for aphid colonies; and H. G. Gaimari, for help in maintaining insect cultures. The authors also thank F. E. Gilstrap and L. K. McKinnon, of the biological control facility at Texas A&M University, for initially supplying the live colony of *Leucopis ninae,* and D. R. Prokrym, USDA-APHIS National Biological Control Laboratory, Niles, Michigan, for *L. ninae* release information, and V. N. Tanasijtshuk, Zoological Institute, Russian Academy of Sciences, St. Petersburg, for identifying the chamaemyiids. For reviewing the manuscript, the authors thank: L. Carloye, University of Illinois; C. R. Nelson, University of Texas at Austin; and one anonymous reviewer. This work was funded by Washington state grants of K. S. Pike (11D-3343-1337) and W. J. Turner (10A-3043-0635).

Literature Cited

Babaev, T. B. and V. N. Tanasijtshuk. 1971. The predatory fly *Leucopis (Leucopomyia) alticeps* (Diptera, Chamaemyiidae), its biology and food relations. Zoologicheskii Zhurnal 50: 1520–1529. (In Russian.)

Balch, R. E. 1952. Studies of the balsam woolly aphid, *Adelges piceae* (Ratz.), and its effects on balsam fir, *Abies balsamea* (L.) Mill. Canadian Department of Agriculture, Publication 867.

Balch, R. E., R. C. Clark, and N. R. Brown. 1956. *Adelges piceae* (Ratz.) in Canada with reference to biological control. Proceedings of the 10th International Congress of Entomology 4: 807–817.

Barber, K. N. 1984. A revision of *Pseudodinia* Coquillett (Diptera: Chamaemyiidae). M.S. thesis. Department of Environmental Biology, University of Guelph, Guelph, Ontario. 212 pp.

———. 1985. Taxonomic revision of the genus *Pseudodinia* Coquillett (Diptera: Chamaemyiidae). Proceedings of the Entomological Society of Ontario 116: 105–167.

Beingolea, O. 1957. Notes on a chamaemyiid (Diptera) predator of the eggs of *Orthezia insignis* Douglas (Homoptera) in Peru. Bulletin of the Brooklyn Entomological Society 52: 118–121.

Bennett, F. D. 1961. The taxonomy, biology, and parasites of some California species of *Leucopis* (Chamaemyiidae: Diptera). Ph.D. dissertation. Department of Entomology, University of California. 233 pp.

Brown, N. R. and R. C. Clark. 1957. Studies of predators of the balsam woolly aphid, *Adelges piceae* (Ratz.) (Homoptera: Adelgidae). IV. *Neoleucopis obscura* (Hal.) (Diptera: Chamaemyiidae), an introduced predator in eastern Canada. Canadian Entomologist 89: 533–546.

Cherian, M. C. 1933. An agromyzid fly predaceous on aphids. Madras Agricultural Journal 21: 343–344.

Clark, R. C. and N. R. Brown. 1957. Studies of predators of the Balsam woolly aphid, *Adelges piceae* (Ratz.) (Homoptera: Adelgidae). III. Field identification and some notes on the biology of *Neoleucopis pinicola* Mall. (Diptera: Chamaemyiidae). Canadian Entomologist 89: 404–409.

Cottam, R. 1922. Notes on the bionomics of an aphidophagous fly of the genus *Leucopis* in the Anglo-Egyptian Sudan. Entomologist's Monthly Magazine 58: 61–64.

Culliney, T. W., J. W. Beardsley, Jr., and J. J. Drea. 1988. Population regulation of the Eurasian pine adelgid (Homoptera: Adelgidae) in Hawaii. Journal of Economic Entomology 81: 142–147.

Delucchi, V. and H. Pschorn-Walcher. 1954. *Cremifania nigrocellulata* Czerny (Diptera, ?Chamaemyiidae), ein raüber an *Dreyfusia (Adelges) piceae* Ratz. (Hemiptera, Adelgidae). Zeitschrift für Angewandte Entomologie 36: 84–107. (In German.)

Eichhorn, O. 1968. Problems of the population dynamics of silver fir woolly aphids, genus *Adelges* (= *Dreyfusia*), Adelgidae. Zeitschrift für Angewandte Entomologie 61: 157–212.

Gaimari, S. D. 1991. Use of silver flies (Diptera Chamaemyiidae) for biological control of homopterous pests. Proceedings of the Washington State Entomological Society 53: 947–950.

———. 1993. Comparative life histories and morphology of the immature stages of three *Leucopis* spp. (Diptera: Chamaemyiidae), and methods for rearing *Leucopis.* M.S. thesis. Department of Entomology, Washington State University, Pullman, Washington. 120 pp.

Gaimari, S. D. and W. J. Turner. 1996. Immature stages of *Leucopis ninae* and two variant populations of *Leucopis gaimarii* (Diptera: Chamaemyiidae) feeding on the Russian wheat aphid, *Diuraphis noxia* (Homoptera: Aphididae). Proceedings of the Entomological Society of Washington 98: 647–666.

Greathead, D. J. 1995. The *Leucopis* spp. (Diptera: Chamaemyiidae) introduced for biological control of *Pineus* sp. (Homoptera: Adelgidae) in Hawaii: implications for biological control of *Pineus*

?boerneri in Africa. The Entomologist 114: 83–90.

Large, E. C. 1954. Growth stages in cereals. Plant Pathology 3: 128–129.

Maple, J. D. 1934. The biology of the genus *Leucopis* (Diptera). M.S. thesis. University of California. 132 pp.

McAlpine, J. F. 1971. A revision of the subgenus *Neoleucopis* (Diptera: Chamaemyiidae). Canadian Entomologist 103: 1851–1874.

———. 1977. A remarkable new species of *Leucopis* from western Canada (Diptera: Chamaemyiidae). Canadian Entomologist 79: 14–18.

———. 1978. A new dipterous predator of balsam woolly aphid from Europe and Canada (Diptera: Chamaemyiidae). Entomologica Germanica 4: 349–355.

McAlpine, J. F. and V. N. Tanasijtshuk. 1972. Identity of *Leucopis argenticollis* and description of a new species (Diptera: Chamaemyiidae). Canadian Entomologist 104: 1865–1875.

Mills, N. J. 1990. Biological control of forest aphid pests in Africa. Bulletin of Entomological Research 80: 31–36.

Nakao, H. K., G. Y. Funasaki, S. Y. Higa, and P. Y. Lai. 1981. Introductions for biological control in Hawaii—1977 and 1978. Proceedings of the Hawaiian Entomological Society 23: 425–430.

Prokrym, D. R., D. J. Nelson, G. S. Sauter, and C. J. Copeland. In press. Russian wheat aphid biological control project, FY 1994 project report. U.S. Department of Agriculture, Animal and Plant Health Inspection Service Report.

Raspi, A. 1983. Contributi alla conoscenza dei Ditteri Camemiidi. II. Note etologiche e morfologiche su *Leucopis interuptovittata* Aczél, *Chamaemyia flavipalpis* (Haliday) e *Parochthiphila coronata* (Loew) (Diptera, Chamaemyiidae) della toscana litoranea. Frustula Entomologica, nuova serie 6: 1–37. (In Italian, English summary.)

Sandhu, G. S. and K. K. Kaushal. 1975. Biological studies and host range of *Leucopis* sp. (Chamaemyiidae: Diptera), a predatory fly on aphids in the Punjab. Indian Journal of Entomology 37: 185–187.

Sluss, T. P. and B. A. Foote. 1971. Biology and immature stages of *Leucopis verticalis* (Diptera: Chamaemyiidae). Canadian Entomologist 103: 1427–1434.

Sluss, T. P. and B. A. Foote. 1973. Biology and immature stages of *Leucopis pinicola* and *Chamaemyia polystigma* (Diptera: Chamaemyiidae). Canadian Entomologist 105: 1443–1452.

Stevenson, A. B. 1967. *Leucopis simplex* (Diptera: Chamaemyiidae) and other species occurring in galls of *Phylloxera vitifoliae* (Homoptera: Phylloxeridae) in Ontario. Canadian Entomologist 99: 815–820.

Tanasijtshuk, V. N. 1959. Species of *Leucopis* Mg. (Diptera, Chamaemyiidae) from the Crimea. Entomologicheskoye Obozreniye 38: 923–940. (In Russian; English translation, 1959, Entomological Review of Washington 38: 829–844.)

———. 1961. Arten der Gattung *Leucopis* aus dem nördlichen Kaukasus (Diptera, Chamaemyiidae). Beiträige zur Entomologie 11: 872–889. (In German, English summary.)

———. 1962. New and little-known species of the genus *Leucopis* (Diptera, Chamaemyiidae) from the European part of the USSR. Entomologicheskoye Obozreniye 41: 220–229. (In Russian; English translation, 1962, Entomological Review of Washington 41: 132–138.)

———. 1963. Biology of the genus *Parochthiphila* Czerny (Diptera: Chamaemyiidae). Zoologicheskii Zhurnal 43: 1876–1888. (In Russian, English summary.)

———. 1965. *Leucopomyia* species (Diptera: Chamaemyiidae) of the USSR fauna. Zoologicheskii Zhurnal 44: 1202–1213. (In Russian, English summary.)

———. 1968. Palearctic species of the genus *Parochthiphila* (Diptera, Chamaemyiidae). Entomologicheskoye Obozreniye 47: 633–651. (In Russian; English translation, 1968, Entomological Review of Washington 47: 388–399.)

———. 1970a. Contributions to the knowledge of the Chamaemyiidae (Diptera) of Poland. Fragmenta Faunistica 16: 123–143. (In Russian, English summary.)

———. 1970b. Palearctic species of the genus *Chamaemyia* Panzer (Diptera, Chamaemyiidae) from the collection of the Zoological Institute, USSR Academy of Sciences. Entomologicheskoye Obozreniye 49: 227–243. (In Russian; English translation, 1970, Entomological Review of Washington 49: 128–138.)

———. 1972. New species of the genus *Leucopis* Mg. (Diptera, Chamaemyiidae) from central Asia. Entomologicheskoye Obozreniye 51: 644–661. (In Russian; English translation, 1972, Entomological Review of Washington 51: 395–398.)

———. 1986. Silver-flies (Chamaemyiidae). Fauna of the USSR, new series 134, Dipterans. Volume 14, 7. Zoological Institute of the Russian Academy of Sciences. Nauka Publishers, St. Petersburg. 336 pp. (In Russian.)

———. 1996. Two species of *Leucopis* (Diptera: Chamaemyiidae) predacious on the Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Homoptera: Aphididae), in North America. Proceedings of the Entomological Society of Washington 98: 640–646.

Tawfik, M. F. S. 1965. The life history of *Leucopis puncticornis aphidivora* Rond. Bulletin de la Société Entomologique de France 49: 47–57.

Tiensuu, L. 1951. Notes on the smallreed coccid, *Er-*

iopeltis lichtensteini Sign. (Hem., Coccoidea, Lecanoidae) and its natural enemies in Finland. Annales Entomologici Fennici 17: 3–10.

Tracewski, K. T. 1983. Description of the immature stages of *Leucopis* sp. nr. *albipuncta* (Diptera: Chamaemyiidae) and their role as predators of the apple aphid, *Aphis pomi* (Homoptera: Aphididae). Canadian Entomologist 115: 735–742.

Valenti, M. A. and S. D. Gaimari. 1992. The manzanita leafgall aphid, *Tamalia coweni* (Cockerell) (Homoptera: Aphididae), and its association with the predator *Leucopis* sp. (Diptera: Chamaemyiidae). Proceedings of the Washington State Entomological Society 54: 972–977.

Wilson, F. 1938. Notes on the insect enemies of chermes with particular reference to *Pineus pini,* Koch, and *P. strobi,* Hartig. Bulletin of Entomological Research 29: 373–389.